Mechanical Energy Oscillations of Two Brachiation Gaits: Measurement and Simulation

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ABSTRACT How do arm-swinging apes locomote effectively over a variety of speeds? One way to reduce the metabolic energy cost of locomotion is to transfer energy between reversible mechanical modes. In terrestrial animals, at least two transfer mechanisms have been identified: 1) a pendulum-like mechanism for walking, with exchange between gravitational potential energy and translational kinetic energy, and 2) a spring-like mechanism for running, where the elastic strain energy of stretched muscle and tendon is largely returned to reco- accelerate the animal. At slower speeds, a brachiator will always have at least one limb in contact with the support, similar to the overlap of foot contact in bipedal walking. At faster speeds, brachiators exhibit an aerial phase, similar to that seen in bipedal running. Are there two distinct brachiation gaits even though the animal appears to simply swing beneath its overhead support? If so, are different exchange mechanisms employed? Our kinetic analysis of brachiation in a white-handed gibbon (Hylobates lar) indicates that brachiation is indeed comprised of two mechanically distinct gaits. At slower speeds in “continuous contact” brachiation, the gibbon utilizes a simple pendulum-like transfer of mechanical energy within each stride. At faster speeds in “ricochetal” brachiation, translational and rotational kinetic energy are exchanged in a novel “whip-like” transfer. We propose that brachiators utilize the transfer between translational and rotational kinetic energy to control the dynamics of their swing. This maneuver may allow muscle action at the shoulder to control the transfer and adjust the ballistic portion of the step to meet the requirements for the next hand contact.

Brachiation is a suspensory form of locomotion where the animal supports its weight with its thoracic limbs beneath a superstrate (usually tree branches). Gibbons are a highly specialized genus of small ape that depend on brachiation for up to 80% of their total locomotion (Andrews and Groves, 1976). Brachiation has been described as pendulum-like, because the animal swings in an arc beneath its handhold at the end of its extended limb. Pendulum-like exchange of potential and kinetic energy has only recently been directly demonstrated in brachiating apes (Chang et al., 1997), though many similarities have been recognized between the motions of a simple, unforced pendulum model and that of gibbon and siamang brachiation. These observations led to the assumption that pendular energy exchange is a determinant of brachiation dynamics (Andrews and Groves, 1976; Ashton and Oxnard, 1964; Avis, 1962; Carpenter, 1976; Chivers, 1974; Fleagle, 1974; Jenkins et al., 1978; Jungers and Stern, 1984; Mittermeier, 1978; Parsons and Taylor, 1977; Preuschoft and Demes, 1984).

Successful negotiation of the complex forest canopy requires a high degree of controlled movement and a wide range of speeds. Although the pendulum provides advantages in conserving energy in oscillatory motion, it has the distinct disadvantage of restricting the oscillation frequency. Stride frequency influences forward velocity in brachiators just as it does in terrestrial walkers and runners. The natural period of a pendulum is determined by the distribution of mass around the pivot (which is largely determined by the length of the support arm) and the downward acceleration due to gravity. Oscillation frequency will be determined by the distribution of mass within a swinging animal, since gravitational acceleration can be considered a constant. It is possible for an animal to redistribute its mass by altering the position of its nonsupporting arm and pelvic limbs (Fleagle, 1974), but this can only provide a relatively small redistribution of total mass. Driving a pendulum at frequencies beyond its natural frequency requires substantial investment of energy (Hildebrand, 1985). It is difficult to imagine how a simple pendular system could allow the changes in...
velocity necessary for a gibbon to negotiate its highly complex environment (Swarz, 1989).

Substantially different constraints act on the brachiator compared to terrestrially moving animals. Along with the obvious reversal in orientation of the limbs relative to the action of gravity, one of the main constraints on brachiation is the requirement to readily adapt to different distances between support contacts. In contrast to the terrestrial situation in which the animal can usually depend on locating an appropriate support near where the stride cycle would place the limb, the three-dimensionally complex world of the brachiator means that the dynamic motion of the animal’s limb system and center of mass oscillations must be readily adaptable to ever-changing support opportunities. In higher-speed travel, the gibbon employs both a contact and a flight phase in its gait (Hollhin, 1984). This is termed “ricochetal” brachiation. We have shown that a critical determinant of ricochetal brachiation is the coordination of the end of the flight phase with the beginning of the following contact phase (Bertram et al., 1999). Mechanical energy can be retained in the ricochetal gait if the parabolic arc of the flight phase is tangent with the circular arc of the contact phase swing at initial hand contact. This eliminates energy losses due to the mechanical collision between the animal and its support. The flight path must be largely controlled prior to the initiation of the preceding ballistic flight phase of the stride, while the animal is in contact with the previous handhold. But how is the brachiator able to accomplish this mechanical control during active brachiation and satisfy this requirement?

As the initial step in answering this question, we employed a kinetic evaluation of brachiation and compared mechanical behavior under varying handhold spacings. We developed a transducer for measuring reaction force applied by the hand of a brachiating gibbon as it moved along a series of handholds affixed to the roof of an exercise cage (Chang et al., 1997), and used the measured forces to calculate the influence of hand contact on the motion of the animal’s mass. Once we determined the mechanics of brachiation, we then developed simple computational models to simulate brachiation and verify our interpretation of the observed motions and the mechanical interactions with the support.

**METHODS AND MATERIALS**

We investigated the dynamics of brachiation at different speeds in a 7.95-kg, female white-handed gibbon (*Hylobates lar*). The animal was free to brachiate at its preferred speed, but the spacing of the handholds (0.80, 1.20, 1.60, 1.72, 1.95, and 2.25 m) strongly influenced the animal’s choice of forward velocity (Table 1). The animal employed ricochetal brachiation at handhold spacings of 1.6 m or greater.

Using analysis methods analogous to those used in terrestrial locomotion (Cavagna, 1975; Cavagna et al., 1976, 1977), the velocity and position of the gibbon’s center of mass (CM) were estimated by taking single and double integrations of the animal’s acceleration (determined from force applied to the instrumented handhold during hand contact). Integration constants were found by assuming periodic motion. Gravitational potential energy ($E_p = mgh$) and translational kinetic energy ($E_K = 1/2 m v^2$) were then calculated from these values. See our previous work for full explanations of these standard techniques as applied to brachiation (Chang et al., 1997, 2000).

Percent mechanical energy recovery is a measure of the effectiveness of the exchange between $E_p$ and $E_K$ (Cavagna et al., 1976; Full et al., 1991). We calculated this exchange for the gibbon using the relation

$$\% \text{ recovery} = \left( \frac{\Sigma \Delta E_p + \Sigma \Delta E_K - \Sigma \Delta E_{tot}}{\Sigma \Delta E_p + \Sigma \Delta E_K} \right) \cdot 100,$$

where $\Sigma \Delta$ = the sum of the positive increments of energy, $E_p$ = gravitational potential energy, $E_K$ = translational kinetic energy, and $E_{tot}$ = total mechanical energy (sum of $E_p$ and $E_K$).

We calculated rotational kinetic energy ($E_{Krot}$) of the body for the 2.25-m handhold spacing, based on observed changes in body orientation of the animal in ricochetal brachiation. Trunk movement was measured from orientation of the thoracic and lumbar spine during the contact (swing) portion of the brachiating swing. Video fields from perpendicular lateral views of the animal’s movement across the handholds were digitized (Panasonic AG-1960 VCR, Data Translation frame grabber card, Power Mac 7100), and the angle of the spine was measured on a field-by-field basis (NIH-Image version 1.57). The measured angles were then plotted against time, and these data were fitted with a fourth-order polynomial ($r^2 = 0.97$). This polynomial was then integrated to estimate angular velocity of the trunk ($\omega$). Mass moment of inertia of the trunk segment (I) was calculated from known mass of the animal (7.95 kg), and volumetric estimates of the major body components were taken from analysis of the dimensionally calibrated video image, assuming a cylindrical form.

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**TABLE 1. Effect of handhold spacing on the mechanics of brachiation**

<table>
<thead>
<tr>
<th>Speed (msec$^{-1}$)</th>
<th>Handhold spacings (m)</th>
<th>Number of runs</th>
<th>Time of hand contact(s)</th>
<th>Percent recovery</th>
</tr>
</thead>
<tbody>
<tr>
<td>0.63 (0.45)</td>
<td>0.80</td>
<td>11</td>
<td>1.56 (0.45)</td>
<td>57.7 (14.0)</td>
</tr>
<tr>
<td>1.31 (0.24)</td>
<td>1.20</td>
<td>20</td>
<td>0.96 (0.21)</td>
<td>67.4 (18.4)</td>
</tr>
<tr>
<td>1.82 (0.09)</td>
<td>1.60</td>
<td>11</td>
<td>0.67 (0.06)</td>
<td>45.3 (5.2)</td>
</tr>
<tr>
<td>1.98 (0.14)</td>
<td>1.72</td>
<td>19</td>
<td>0.62 (0.05)</td>
<td>49.4 (9.7)</td>
</tr>
<tr>
<td>2.35 (0.15)</td>
<td>1.95</td>
<td>13</td>
<td>0.50 (0.05)</td>
<td>45.8 (9.6)</td>
</tr>
<tr>
<td>2.69 (0.26)</td>
<td>2.25</td>
<td>11</td>
<td>0.48 (0.06)</td>
<td>38.3 (8.3)</td>
</tr>
</tbody>
</table>

$^1$ Values are means and one standard deviation (in parentheses). Continuous contact brachiation is used for 0.8-m and 1.2-m spacings. At 1.6 m and above, brachiation involves a noncontact component and is considered ricochetal.
A density of 100 kg/m³ was used to determine that the support arm mass was 0.95 kg. The rotating trunk segment was assumed to include pelvic limbs and the nonsupport pectoral limb mass (7.0 kg). The length of the support limb was determined to be 0.56 m, total trunk length (l) was 0.62 m (accounting for position of pelvic limbs, see Fig. 2), and mass moment of inertia \( I = ml^{5/3} = 0.556 \text{ kgm}^3 \). Rotational kinetic energy \( E_{Krot} \) was calculated as \( E_{Krot} = \frac{1}{2} l \omega^2 \). Although the values of \( l \) and \( l \) for the “trunk” segment are only rough estimates, they are used here to provide a qualitative approximation of \( E_{Krot} \) for the gibbon in ricochetal brachiation. As the first measure of \( E_{Krot} \), we are primarily interested in the fundamental aspects of the mechanical energy oscillations, rather than specific details. The estimates used are adequate to allow the determination of the general trends in energy changes during the contact period of this animal.

We used a graphics-based physical modeling program (Working Model version 3.0.1, Knowledge Revolution, San Mateo, CA) to verify our interpretation of the dynamics of the brachiating gibbon and simulate passive motions of a model representing the gibbon. We constructed a simple two-dimensional model of the gibbon from which we calculated the interactions with the support and kinetic energy oscillations during the support phase of the stride (comparable to the force transducer measurements and energy determinations derived from them for the brachiating gibbon). The model was composed of two linked segments, a trunk of mass 7.0 kg and length 0.62 m, and a support arm of mass 0.95 kg and length 0.56 m. Our model uses slightly different dimensions and mass distribution than previous models, but borrows heavily on the analysis strategy employed by Saito et al. (1994), Yamazaki (1990), and Preuschoft and Demes (1984).

Two simulations of this model were performed. The first simulated one swing of a continuous contact stride, i.e., one half of the full stride cycle (Fig. 1C). Initial velocity was set to zero in both the ver-

Fig. 1. Comparison of a gibbon using continuous contact brachiation with a simulation of an inert, jointed pendulum of comparable mass and dimension. A: Sequential outlines of the gibbon during one swing. B: Potential and kinetic energy changes during the swing depicted in A. C: Sequential outlines of the simulated jointed pendulum during one swing. D: Potential and kinetic energy oscillations calculated from the simulation. Traces of the animal’s position are taken from video records at 0.1-sec intervals. The center of mass position is shown as an open circle in the simulation. The transducer-determined positional changes of the center of mass of the gibbon are indicated by the bold line through the swing sequence.
tical and horizontal directions. The angle of contact was set to 45° relative to vertical. This angle has been shown to provide optimum conditions for brachiation travel (Bertram et al., 1999). The second simulation placed the trunk segment at a different angle than the arm segment, to replicate the orientation of the segments during ricochetal brachiation (Fig. 2C). The initial velocity was set to 2.5 ms\(^{-1}\) in the horizontal direction of travel, and 3.0 ms\(^{-1}\) downward in the vertical direction. These initial velocities are those expected at initial contact in ricochetal brachiation for a handhold spacing of 2.25 m. The simulations were set to calculate \(E_P\), \(E_K\), and \(E_{\text{Krot}}\). The simulation outputs were then compared to these factors determined from the kinetics and kinematics of the brachiating gibbon at each gait. Although the simulations are quite simple and do not attempt to model the entire gait cycle, they do provide an estimate of the passive mechanical energy oscillations of a two-link system resembling the mass distribution of the gibbon. The purpose of the simulation is to compare the directly measured forces and motions of the gibbon with an unconstrained passive model. The result will indicate that portion of the energetic exchange that can be passively determined in the gibbon.

**RESULTS**

At spacings of 0.8 m and 1.2 m, the gibbon’s trunk and legs swing in unison with the support arm (Fig. 1A). At these slower speeds, the gibbon uses a continuous contact gait and swings much like a simple pendulum. This impression is verified by the out-of-phase relationship of \(E_K\) and \(E_P\) during the hand contact in this gait (Fig. 1B).

At handhold spacings above 1.2 m (1.6, 1.72, 1.95, and 2.25 m), the gibbon has a portion of the stride in which there is no hand contact and the animal traverses the space between handholds via a ballistic flight phase. This behavior has been documented...
in the wild and is commonly referred to as ricochetal brachiation. Many aspects of the superstrate reaction force in ricochetal brachiation are similar to those of continuous contact brachiation. However, vertical force is greater in ricochetal brachiation (Chang et al., 2000). The increase in vertical force matches a correlated decrease in hand contact time at the higher forward velocities of ricochetal brachiation. In order for the animal to maintain a constant average height (i.e., if the handholds are arranged on the same level), it is necessary for the upward oriented vertical impulse ($F dt$) applied to the handhold to match the downward oriented impulse of gravity over the stride cycle (which includes both the support and flight portions of the locomotion cycle). As the time available to apply the upward impulse during hand contact decreases at higher forward velocities, the animal must compensate with greater vertical force in order to maintain the same vertical impulse.

In ricochetal brachiation, the $E_p$ oscillation is similar in form and magnitude to that of continuous contact brachiation (compare Fig. 1B and 2B). This simply indicates that in both gaits, the animal swings below its extended arm. In contrast to continuous contact brachiation, however, the shape of the $E_K$ curve in ricochetal brachiation is substantially different. Rather than a smooth increase and decrease as is seen for continuous contact brachiation, there is a local minimum in $E_K$ evident at mid-support in ricochetal brachiation (Fig. 2B).

The local minimum in $E_K$ is observed for all brachiation runs with a handhold spacing above 1.2 m. At these spacings there is a ballistic flight phase evident, and the animal employs a ricochetal gait. We noticed that the relative magnitude of the local minimum in the $E_K$ curve increases with handhold spacing and with forward velocity (Fig. 3). Percent recovery, or the degree of pendular $E_p - E_K$ exchange, reaches a maximum at the 1.2 m handhold spacing where the mean recovery is 67.4% ($±18.4\%$) (Table 1). Some continuous contact runs at this spacing displayed percent recovery values in the 90% range. However, for spacing either less than or greater than 1.2 m, percent recovery decreases. Percent recovery appears to be maintained at the 40–50% range for ricochetal brachiation, indicating that these animals are not particularly good pendula at these velocities and handhold spacings, at least in terms of the simple $E_p - E_K$ exchange that this calculation is designed to determine.

Rotational kinetic energy of the trunk of the ricochetal brachiating gibbon shows a maximum at the bottom of the swing (Fig. 2B). This is similar to the situation found for the simulation (Fig. 2D). In the simulation, the $E_K - E_{Krot}$ transfer accounts for 100% of the decrease in $E_K$ as the trunk segment of the model is whipped around the shoulder axis at the bottom of the ricochetal swing. For the gibbon measurements, this transfer accounts for approximately 50% of the $E_K$ decrease.

An important indication of the fundamental difference between continuous contact and ricochetal brachiation can be seen by following the path of the CM during hand contact. In continuous contact brachiation, the CM follows a smooth arc (Fig. 1A) that is similar to that of a free-swinging simple pendulum (Fig. 1C). In ricochetal brachiation, the CM follows a distinctive “V”-shaped path (Fig. 2A). Simulation of the passive motion of a double pendulum provides insight into why the V path occurs. At the bottom of the swing, the rotational velocity of the trunk increases as the support arm stops the downward motion of the shoulder. The trunk is whipped around the shoulder and creates the small radius arc at the bottom of the ricochetal swing (Fig. 2B,C). Although this particular path could be explained by complex muscle actions, our simulations indicate that it is also possible to explain these results as a consequence of passively determined motions, at least in the first half of the swing. At this point we do not have direct measurements that can distinguish between these two alternatives.

**DISCUSSION**

Terrestrial animals moving on legs use a pendulum-like exchange of $E_K$ and $E_P$ to conserve energy at walking speeds (Cavagna and Kaneko, 1977; Full...
During running, this “inverted pendulum” mechanism is abandoned in favor of a spring-like mechanism where $E_K$ and $E_P$ increase and decrease in phase with each other and are transferred to strain energy stored in the elastic components of the limbs (Alexander and Bennet-Clark, 1977; Alexander, 1988). Terrestrial running is characterized by the center of mass being lowest at mid-support and the duty factor of the foot (proportion of the stride that the foot is on the ground) being less than 0.5, indicating a non-contact, or aerial phase to the stride. With respect to the duty factor, the transition from continuous contact to ricochetal brachiation might be considered analogous to the walk-run transition in terrestrial runners (Chang et al., 2000). However, in brachiation, the $E_K$ does not oscillate in phase with $E_P$, even though a local minimum in the $E_K$ curve corresponds to a minimum in $E_P$ (Figs. 2, 3).

It might be tempting to view the “in phase” component of the $E_K$ curve as analogous to the in phase $E_K$ and $E_P$, indicative of strain energy storage in terrestrial running gaits. Unfortunately, the analysis method commonly used for terrestrial systems, which focuses only on translational $E_K$, is not sufficient for this case because in brachiation there is substantial rotational kinetic energy ($E_{Krot}$) that should not be neglected. At ricochetal speeds, the gibbon’s support arm and trunk begin to swing at different rotational velocities. The gibbon dives into the ricochetal hand contact with the trunk initially oriented horizontally and the arm hyperextended above the shoulder (Fig. 2A). As the animal falls to the limit of its arm, the shoulder is sharply decelerated. This can be seen in the sequence of outlines in Figure 2A. The outlines are from individual fields taken at intervals of 0.1 sec. Thus, the translational and rotational velocity is evident from the displacement occurring between each image. Note the hyperextension of the shoulder as the animal moves from initial contact through the first half of the swing. The rate of rotational velocity of the trunk increases as the animal nears the bottom of the swing, while the rotational velocity of the arm decreases until it reaches a minimum near the bottom of the swing. This can be compared to the motion of the passive compound pendulum simulation (Fig. 2B). In the simulation, the large component representing the trunk increases rotational velocity until it reaches a maximum at the bottom of the swing. The rotational velocity of the component representing the arm in the simulation also slows as it approaches the bottom of the swing. In the simulation, the arm segment is actually moved back slightly (counter to the original direction of motion) as a result of rotational momentum of the larger trunk segment. The double pendulum motion results in the path of the CM of the ricochetal gibbon traveling in a characteristic V shape, substantially different from the smooth curve of the pendular swing of continuous contact brachiation. The simulation shows a very similar V-shape trajectory, even without any active components in the model.

As the shoulder decelerates the trunk, translational kinetic energy is converted to rotational kinetic energy (about the gibbon’s center of mass), and the trunk appears to be “whipped” about the shoulder. Our calculations of rotational kinetic energy of the gibbon show that $E_{Krot}$ accounts for up to 50% of the $E_K$ decrease at mid-support, and it occurs 180° out of phase with the $E_K$ (Fig. 2B). The remaining mechanical energy unaccounted for by $E_{Krot}$ is likely either absorbed by the muscles, stored as elastic strain energy, or dissipated in other ways. Although unaccounted for in the current analysis, it is possible that this energy is not lost and could be utilized in other portions of the gait cycle.

The transition between $E_P$ and $E_K$ in walking, or the $E_P$ and $E_{Krot}$ exchange with elastic strain energy in terrestrial running, recover energy that would otherwise be lost to the animal and that would have to be recreated through metabolically costly muscular effort (Cavagna et al., 1977). It is difficult to imagine how the transition of $E_K$ to $E_{Krot}$ could benefit the energetic balance in brachiation, because any real exchange (i.e., not based on ideal assumptions) will result in some degree of energy loss. Since $E_K$ results in translational movement of the animal and in brachiation its direction can be controlled without an intervening conversion to elastically stored energy (see Bertram et al., 1999), it may appear that there is no advantage to making this conversion, and that the exchange of $E_K$ to $E_{Krot}$ is futile.

If energy storage under noncollision circumstances is not a consideration, what then is the explanation of the $E_K - E_{Krot}$ exchange? We previously demonstrated that the effectiveness of the ricochetal brachiation strategy lies in the ability of the animal to determine its next ballistic flight phase in preparation for satisfying the noncollision criterion of the next contact. The reversed relationship between the brachiator and its support allows the animal to move through vertical oscillations via smooth transitions of the body’s motion without direct impact and the use of elastic energy storage. The main determinant of effective ricochetal brachiation is the coincidence of the trajectory of the ballistic portion of the stride with the arc of the swing phase at initial contact (Bertram et al., 1999). This avoids a mechanical collision between the two interacting components of the system (the brachiating animal and its support), and no energy, elastic or otherwise, need be transferred. If the animal is to swing beneath its support with an extended arm and with the axis of the body in line with the axis of the arm, then the only means of controlling the ballistic trajectory of the flight phase of the stride would be in the timing of the hand release. The large moment arm between the center of mass of the body and the hand grip, where the pivot of the rotation takes place, makes it very difficult for the animal to use muscular effort to control the swing motion at the
handgrip. However, if the animal uses a double pendulum strategy and passively converts $E_K$ of the trunk to $E_{Krot}$ in the first half of the swing, then the substantial musculature of the shoulder is in a position to control the reconversion of $E_{Krot}$ to $E_K$. The control of the swing will occur in the second half of contact as the animal prepares for and anticipates the next contact (Fig. 2). We postulate that the passive $E_K - E_{Krot}$ conversion is created in ricochetal brachiation in order to provide the opportunity for the animal to actively control the reconversion of $E_{Krot}$ to $E_K$ (Bertram et al., 1999).

Our previous work showed that it is theoretically possible for brachiators to move ricochetically without energy loss and without depending on standard pendular $E_p$ to $E_K$ exchange to accomplish this (Bertram et al., 1999). In this paper, we suggest that brachiators can use an exchange between translational and rotational kinetic energy to facilitate control of motion with mechanically more advantageous muscle groups, i.e., using those muscles that attach the proximal limb to the trunk rather than the distal muscles that influence the interaction between the animal and its contact at the handhold directly. We suggest that this $E_K$ to $E_{Krot}$ interchange manifests as the specific relative motions of the trunk and the support limb in ricochetal brachiation. We anticipate that this will also affect the path of the CM while the animal contacts the handhold, reasoning that if, after Bertram et al. (1999), mechanical energy during contact with the handhold is considered constant, i.e.,

$$E_K + E_{Krot} + E_p = \text{constant},$$

then an exchange between $E_K$ ($1/2 \, m v^2$) and $E_{Krot}$ ($1/2 \, I_o \dot{\theta}^2$) will influence the velocity of the CM and, as a consequence, its path.

Note that the simulation differs from the gibbon behavior only in the second half of the swing, i.e., after the trunk has passed beneath the handhold. Since the simulation is completely passive, this suggests that the first half of the gibbon swing is dominated by passive motions, while the expected passive motions are altered in the second half of the swing by muscle action. The rotational motion that occurs at the shoulder (relative motion between the axis of the arm and the axis of the trunk segments) is halted at the bottom of the swing and is gradually reversed during the second half of the swing. This suggests that the shoulder is stabilized and controlled by muscle activity in the second half of the swing. This could result in a conversion of the $E_{Krot}$ of the trunk to translational $E_K$ mediated through the action of the large muscles surrounding the shoulder. Previous studies did not focus on this aspect of the conversion of rotational and translational energy in ricochetal brachiation, nor did they pay attention to whether the animals are accelerating or decelerating. However, electromyographic studies of the shoulder muscles indicate that their activity is generally consistent with this model of the ricochetal swing (Jungers and Stern, 1981).

This postulate offers a new perspective on ricochetal brachiation that can form the basis of a reinterpretation of the function of the unique proportions of the brachiating apes and the role of arm and trunk muscle activity in brachiation. It may be tempting to review previous reports of muscle activity in brachiating gibbons to evaluate this hypothesis. Some caution must be taken in doing so, however. The proposed function of the trunk musculature in controlling the ballistic arc of the following brachiation step means that careful consideration must be taken of the precise dynamics of the runs being analyzed. That is, from this perspective, one of the main functions of the musculature connecting the limb to the trunk would be to assist in the acceleration or deceleration of the animal to prepare it appropriately for the following flight phase and subsequent contact. These accelerations and decelerations may be subtle, but in order to interpret the role of these muscles in generating (acceleration) or absorbing (deceleration) energy, it is necessary to strictly monitor the animal’s acceleration and deceleration across its handholds. Currently there are no reports available in the literature that indicate the activity of pectoral girdle musculature while monitoring subtle changes in acceleration or deceleration within a brachiation step.

In this study, we used a simple model of the passive motions of the gibbon’s trunk and arm to verify our interpretation of the kinetics of the two gaits these animals employ. We acknowledge that we have available only one animal trained to brachiate using our analysis system. We attempted to compensate for this by demonstrating, using simple models, that many of the observed motions and energy oscillations are those expected for a passive swinging system under similar circumstances. Although our models only predict the passive action of the animal, the simplicity of the models, and the degree to which the predicted behavior matches that observed, are compelling evidence that our mechanical interpretations are physically reasonable. Note, however, that some substantial differences exist between the kinematics of the gibbon and the model in the ricochetal swing (Fig. 2). The swing of the passive model is symmetric about its midpoint (i.e., the bottom of the swing). The ricochetal swing of the gibbon is asymmetric in that the orientation of the trunk is horizontal at initial hand contact, but vertical at hand release. We interpret this difference as indicating the influence of shoulder muscle activity. Activity in the muscles suspending the pectoral limb of the gibbon has not been measured while the animal brachiates at such large handhold spacings, so our interpretation cannot be directly verified at this time. However, it is possible to generate a similar asymmetry in the ricochetal model by adding a shoulder spring that prevents flexion at the shoulder in the second half of the swing.
Our quantitative analysis of the mechanics of brachiation provides insight into one of the less obvious aspects of this novel locomotory system. Apart from the reversal of orientation of the support and gravitational vector relative to terrestrial locomotion, the uniqueness of brachiation is in the constraints imposed by the three-dimensionally complex and inconsistent support opportunities. Within the forest canopy, the animal must have available the mechanical strategies that will allow it to effectively (and economically) adjust its stride dynamics with every movement it makes. This applies fundamentally different constraints than are seen in terrestrial locomotion. Our studies provide a mechanical explanation for how this is effectively and elegantly accomplished in the gibbon. These studies also provide a new and much more complete perspective on the mechanics of brachiation than has previously been available. This understanding will be essential in evaluating the morphological basis of this unique locomotion strategy and the adaptive processes that led to its existence.

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LITERATURE CITED